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Development of  
*Manicaria arcuata*.

By Henry V. Wilson.





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On the Development of *Manicira areolata*.

By Henry V. Wilson.

During the spring of 1887 the Marine Laboratory, of the Johns Hopkins University was stationed on the island of New Providence, Bahamas. As soon as possible after my arrival, Mar. 6, I endeavored to find out what corals were breeding. Of half a dozen species examined only one was with eggs. This was the so-called Chalk stone or *Manicira areolata*, one of the commonest corals in the Bahama waters. The breeding continued to be very active until the middle of April, when it began to decline coming to a close before the first of May.

The coral is found in large numbers in water of easy wading depth, lying with its pedicel buried in the sand. It lives very well in small aquaria, if care be taken to change the water twice a day. In rearing the larvae I was compelled to employ the same tedious method as











It is evident that the mother gives birth to larvae which  
crawl out by the mouth. But the first two larvae  
of corals I have reared out on a strand and of  
corals and sponges. Each batch numbered in the  
corals, was distributed into four aquaria, and  
was reared in the same way. The first batch was  
in the water of the 1st. The second in the water  
of the 2nd. The 3rd. of March. I was not able to keep  
a third batch until the 1st. of April. I was  
unable to keep a fourth batch until the 1st. of May.  
The larvae stage. The hatching of eggs and  
larvae was probably abnormal, as the eggs  
which I had reared out on a strand and of  
corals and sponges, were not hatched out.  
The larvae stage. The hatching of eggs and  
larvae was probably abnormal, as the eggs  
which I had reared out on a strand and of  
corals and sponges, were not hatched out.  
It is not that fresh after March 20 the  
corals always ejected larvae when set in  
water. The first of larvae hatched out.



The larvae were found to be much more advanced as the season grew later. The larvae on March 21 and 22 were without cilia and in the place represented in Fig. 4, Pl. 1. Those on April 8 were ciliated and as far advanced as Fig. 20, Pl. 3.

The larvae I obtained during March lay for a day or so with their mouths on the surface of the water. They then acquired cilia and began to swim freely about the surface, often collecting in rows at the sides of the tank. I have never observed the same kind of behavior in other species. At the end of a week they had become numerous, and spending most of their time below the surface of the water. When they creep along the bottom and sides of the dish like little worms. Though they are constantly lengthening and tapering, they have the same shape as that of a bee, with the mouth at











Fig. 34, Pl. - , and a longitudinal in Fig. 38.  
The whole mass of larvae received several  
at the same time. In the evening many continued  
to feed a few days until the first part of May.

The lot of larvae I got on the 14th of April  
were born in a more advanced state than their  
predecessors, and developed a little faster  
than the others. So much so, that by the middle of April  
so many of this batch became attached, as of the  
others. This was due to the fact that the lot  
received from me is of a more advanced stage  
of development than the others. This great amount  
of difference amongst the larvae as to the time  
required to reach a certain stage of development  
was due to the fact that the lot received from me  
was of a more advanced stage of development than the others.



a consecutive series of ~~lower~~ stages. When I began  
a section I found that inferences based on the  
results of the earlier stages were very often  
entirely correct.

The first stage was characterized by the  
appearance of a very small, but distinct, shell. At  
this period the first division of the specimen  
was not noticeable. The surface of the  
calcareous matter on the basal surface of the  
attached shells. I was not able to see the  
young corals beyond this point, though I kept  
a few alive until the first of June. The death  
rate increased very much as soon as the corals  
were removed.

# 11. Early Stages including the Formation of layers.

The immediate egg was about as large as the  
young corals of the first stage. The  
corals were very small and very numerous.





The body of the egg was filled with vesicles, re-  
sulting in this respect the ~~body~~ of the juv-  
escence planula. The only observations on the  
segmentation were made on the eggs accidentally<sup>b)</sup>  
discharged Mar. 21. The segmentation started  
near each pole in large numbers. After begin-  
ning the cell division the mass was  
divided into 40 equal blastomeres, which re-  
mained connected by a bridge of tissue. The  
division into four blastomeres then followed. So  
far the segmentation was quite regular, but ir-  
regularities began now to crowd in, which re-  
sulted in the formation of a ~~protrusion~~ ~~small~~  
mass comparable with the irregular planula de-  
scribed by Merz (1901, p. 2) for Iconia. I have  
observed a precisely similar similar segmen-  
tation and planula in an allied medusa, Ur-  
villipus). This irregular mass did not de-  
velop any farther.

The segmentation results in the formation



of a Blastosphere with a very large cavity (Fig. 1). The Blastosphere is markedly bilateral and is without cilia. The cells contain a large number of vacuoles pretty evenly distributed through the cell body. In later Blastospheres (Figs. 2 and 3) the formation of the larval or primitive endoderm has begun. The Blastosphere cells have become decidedly columnar. The nucleus is peripherally placed, and the vacuoles are concentrated in the central end of the cell. The cells are evidently delaminating, the inner vacuolated ends being split off to form the endoderm. The nuclei of the endoderm segments are very hard to make out. The delamination takes place irregularly over the general surface of the Blastosphere, and is of a peculiarly complex character in certain spots. In the cell groups m and m' (Fig. 2, for instance), the lines of the transverse divisions of the several cells are continuous and seem to indicate that the whole group





must have divided transversely while it was  
yet a single cell: i.e. before it had been split-  
up by the longitudinal divisions. But the  
longitudinal divisions clearly show that the  
transverse division did not precede them. Such  
a cell as n Fig 3. throws light on the matter.  
This cell has begun to divide longitudinally, but  
even in the peripheral part of the cell, though the  
longitudinal constrictions are evident enough,  
the segments are far more intimately connected  
than are say n and the adjacent cells. In n' the  
longitudinal division is apparently proper;  
but on comparing the close juxtaposition of the  
new segments, with the marked space between  
n' and the adjacent cells, ~~we~~ I am inclined to  
believe that the halves of n' are still connected  
by bridges of tissue, much as the blastomeres  
in many segmenting eggs remain connected  
after they are clearly ~~run~~ off. In the next  
m' then (Fig 2!) it is probable that the longi-



were the first to appear  
itudinal constrictions ~~first appeared~~ in the mother  
cell, but that before they became complete, <sup>divisions</sup>  
a general transverse constriction took place.

Delamination appears to be the name  
means by which the ~~delamination~~ is formed &  
looked in vain for cells migrating from the  
surface. Whenever there appeared to be such,  
examination of the next sections showed that  
the cells in question had been cut obliquely, the  
periplasmic end with ~~the~~ <sup>the</sup> nucleus having been  
severed from the rest of the cell body. The  
cell a (Fig. 2) for instance, is merely the central  
portion of a constricted cell like b in the  
same figure. The delamination and accompany-  
ing longitudinal division often give rise to  
spherical cells such as x, Fig. 3. These cells  
are always at the surface of the Blastosphere.  
Whether their fate is different from that of the  
general ectoderm cells, I do not know.

The cavity of the Blastosphere are having been filled





up by the endoderm segments, a solid planula, fig. 4, results. On studying this figure, a median longitudinal section, we see that the longitudinal division of the superficial cells which was active in the blastosphere, has given rise to a layer of columnar cells, the ectoderm. The inner ends of these cells are not distinctly marked off from the solid endoderm. The endoderm, when the living larva is compressed or when pretty thick sections are examined, appears made up of a quantity of vesicles which look something like fat-cells. When thin sections are examined it is found there exists a continuous protoplasmic matrix binding the vesicles together, which are now seen to be identical with the vacuoles present in the endoderm segments of the blastosphere cells. There is however a decided difference in their appearance which is not well shown in the figures (4 and 5). In the blastosphere cell the protoplasm in which lie the vacuoles, is tolerably uniform; but in the endoderm of



The planula, the protoplasm immediately round each vacuole has become denser than the intervening stroma, so as to form a more or less differentiated shell for the vacuole. The shell stains much more readily than the stroma. What the contents of the vesicle is, I can not say. Carmine and haematoxylin do not affect it, and in these young stages I did not try osmic acid.

The endoderm contains besides the vacuoles just mentioned, a number of "yellow cells" and scattered nuclei. No cell boundaries can be made out, and there is every appearance of the structures being syncytial. A stage between figs. 2 and 4 would go far towards elucidating the intimate structure of the solid endoderm, but I did not succeed in obtaining such.

While the embryo is still solid, the oesophageal invagination makes its appearance, fig. 4. The lumen is very narrow except at its base where it is <sup>slightly</sup> dilated. The larva at this stage



swims feebly about, the cilia having commenced to develop.

The formation of the permanent layers is illustrated in fig. 5. In the region a the layers are in the condition characteristic of the earlier larva. But in the neighborhood of c the ectoderm cells have become much more clearly marked off from the endoderm. Their inner ends form a ragged line, which gradually becomes more uniform, until the ectoderm is bounded internally by a smooth limiting surface as at b. Though the bounding surface is smooth in this region, the supporting lamella has not yet formed. A little later it appears as a delicate membrane between the two layers (from a transverse mouth!). While it is still very thin it resembles an ordinary cuticle. It appears between the layers, and is not formed by the direct metamorphosis of the ends of ectoderm or endoderm cells. Which layer secretes the membrane, is a ques-





tion which has been incidentally discussed by a number of authors. In early stages such as fig. 5 it is impossible to decide whether the secretion ~~belongs to the~~ is the peculiar property of either layer. But in later stages it is found in places where it can only be endodermic, and in others where it is evidently ectodermic. I shall return to this <sup>point</sup> ~~question~~ <sup>farther on</sup> in the general section. The various steps in the formation of the permanent layers can often be observed, with but few gaps, in a single section. Fig. 5 is such a section with a few additions from another.

~~The formation of the permanent endoderm from the solid or larval endoderm may be described as the condensation of the protoplasm of form a peripheral layer.~~

The permanent endoderm is formed from the larval endoderm by the differentiation of a ~~new~~ peripheral layer from the central portion, (fig. 5). The peripheral layer is not joined continuously



over the whole surface, but in spots here and there. It is at first walled off from the central portion only by its somewhat greater density, but it gradually loses its connection with the latter, acquiring at the same time cell boundaries and a smooth limiting surface. The permanent endoderm as thus formed is a single layer of vacuolated cubical cells, except in the immediate neighborhood of the oesophagus, round the sides of which the cells are massed so as to fill up more or less completely the space between it and the body wall. This is especially noticeable on the left side of fig. 5.

The oesophageal invagination as seen in fig. 5 is much dilated at its base. Here the ectoderm has preserved its intimate connection with the endoderm, the ectoderm cells not even having acquired a smooth bounding surface. In fig. 6 this even surface has been acquired, but at no time is a supporting lamella secreted over this



area. The absence of the lamella clearly facilitates the absorption by the endoderm (or yolk) of the base of the invagination. The details of the absorption are as follows. The dilated portion of the invagination, shown in transverse section in fig. 10, is broken through at one point. Through this breach the yolk passes into the lumen (figs. 8-10), and the base of the oesophagus thus enclosed above and below by yolk is absorbed. It is I think possible to recognize the base after it has fused into the yolk, though of course the histological structure is gone. In fig. 8 is seen a curved mass of tissue extending from the left side of the oesophagus nearly to the right. Though in structure like the yolk it stains a much deeper blue, and is therefore quite well defined. On comparing this figure with figs. 6 and 10, there seems to be no doubt that the mass in question really represents the ectoderm base of the oesophagus.

The central portion of the larval endoderm





remains as a fold gold. In fig. 5 it still exists as a continuous structure, but as wave and wave & the protoplasm is drawn into the layer of permanent endoderm, the vesicles lose to a greater or less extent their connection with each other. By the time the layers are definitely established, figs 6 and 8, the gold is a loose mass of vesicles, the walls of which have begun to disintegrate. The vesicular wall or shell is extremely dense, and in this and subsequent stages seems to be fatty as it stains very dark with osmic. Remnants of the gold are found in stages as <sup>late</sup> as fig. 19.

Though the formation of the supporting lamella and the differentiation of the permanent endoderm very often take place at about the same time, this is not always the case. In many larvae the supporting lamella is entirely formed and the respiratory pores opened centrally, while the endoderm is still solid (figs. 10 & 12).



The "yellow cells", which later are found in such abundance, appear for the first time in the planula (fig. 4). I have not seen them actually entering the planula, but in this and slightly older stages, fig 5, a few occur in the superficial ectoderm, whereas in older larvae and in the adults they are confined to the inner layer of the body.

### Comparisons.

#### a. Germinal Layers.

Among the many ways in which the germinal layers are formed within the Coelenterates, Meltschnikoff (2) has picked out what seems to answer the requirements of an ancestral type. In this so-called "mixed delamination", a solid ectoderm is built up both by delamination and by the migration of superficial cells into the interior. Physalia (Meltschnikoff) and better Aurelia (Fottle) are good examples of this process. Accepting this type as ancestral, Manicina has diverged



along the same path as certain Trachomedusae  
(Geryonia, Sirope): i.e. none of the <sup>blastophore</sup> cells migrate  
into the interior, but the endoderm is formed  
exclusively by delamination.

Though the way in which the solid larva was  
originally formed seems preserved in but a ~~few~~  
~~forms~~ <sup>species</sup>, the solid larva itself may fairly be  
considered as typical for the Coelenterates. It  
is especially well preserved in the Hydroids and  
Anthozoa. In one division of the latter group, the  
Alcyonaria, it has been found in all the forms  
studied (with the possible exception of Geryonia),  
and it occurs in the majority of Zoanthoria.

The Alcyonarian which comes nearest to Manicina  
in the formation of its layers is Renella (3!). In this  
~~form~~ <sup>genus</sup> though the blastophore has a very small  
cavity, the endoderm is formed by delamination  
as in the coral. As regards the structure of its  
larval endoderm however, Renella differs con-  
siderably from Manicina. In the inner three en-





endoderm is made up of a mass of cells, of which the  
 peripheral layer becomes the permanent endoderm,  
 while the central cells go to pieces and are proba-  
 bly eaten away in a fashion by the peripheral  
 cells. In Manicaria on the other hand the larval  
 endoderm is a syncytium, and in the entire  
 process which leads up to the formation of the  
 adult endoderm a prominent part is played  
 by the "vesicles", which in all probability contain  
 some kind of yolk. The syncytial nature of the  
 solid endoderm must greatly <sup>accelerate</sup> ~~simplify~~ the  
 development of the <sup>layer</sup> ~~permanent endoderm~~ <sup>there is</sup>  
~~simplex~~ <sup>permanent endoderm</sup> ~~and~~ <sup>and</sup>  
~~also~~. Being of the syncytial nature of the solid  
 endoderm the complete resorption of the latter  
 into the permanent layer must require less time  
 in Manicaria than in Renilla. For in M. there is no  
 large accumulation of yolk cells which must slowly  
 be devoured away in a fashion by the peripheral  
 cells. In the contrary, when the time for the for-  
 mation of the permanent endoderm has arrived,



The general mesoplasm is merely drawn inward to the periphery, and after it has broken up into cells as has been described, there remains but little nutriment in the loose yolk mass. Just how the yolk is ingested after the cellular endoderm is fully formed I am unable to say. It is certainly not devoured ameba-fashion by the endoderm cells at large, though in the region of the oesophagus, figs. 6 & 8, connection is maintained for a considerable time between the yolk and the endoderm, which elsewhere is ~~fully~~ <sup>completely</sup> formed.

Amongst the corals and Actinies two or three forms have been described as undergoing invagination, notably Criarthus (Kovalovsky-4) and Actinia (Jourdain-5). While the mere occurrence of invagination in a Cnidarian group can scarcely be said any longer to have a phylogenetic significance, these two forms are especially interesting, as Wilson has remarked (3 p.), because in each of them a yolk mass appears after the layers have been



completely proved. I have not seen Kowalevsky's figures, but the golt depicted in Jourdain's fig. 9 is precisely like like the golt of a young *Manicina*. making allowance for the difference in thickness of the sections. The a priori improbability that the endoderm would first secrete a golt, Kowalevsky, and then invaginate it again, taken together with the similarity of the golt in question to that of *Manicina*, might tempt one to believe that both authors had mistaken a comparatively late stage with a large and widely open peritrophic for a true gastrula. But Kowalevsky's statements on this head are so definite as to preclude this supposition.

#### b. Supporting Savella.

The only two authors who have described in detail the formation of the supporting Savella are Jourdain (l.c.) and Wilson (l.c.). Jourdain's observations were made on a coral, *Balanophyllia*, and on *Actinia*, *Actinia equina*. He draws a sharp distinction between the "membrane normale" and





and the "jelly". The inner covers the German Stützmembran. It is a fine limiting membrane which appears between the two layers, and extends into the mesenteries & into their axial bands. This is what I have chosen it as the supporting lamella (comp. any of figures on Pl. 3). Its origin Tjurdaire was unable to trace with any certainty. The jelly on the other hand which eventually becomes fibrous is forced outside of the membrana propria by the superficial ectoderm cells. The inner ends of these cells break off and run together to form a granular mass in which fibres subsequently appear (l. c. figs. 119 + 129).

The supporting lamella described by Wilson is evidently the same thing as Tjurdaire's membrana. Its origin according to W. is very similar to the mode of formation just described for the jelly. The inner ends of the ectoderm cells become swollen, constrict off, and form a granular layer which condenses to a smooth membrane. Wilson does not speak of jelly as distinct from the supporting lamella



proper. In Maricinia there is not indeed a very dis-  
 tinct membrane as described. In later larval  
 stages at various spots, especially in angles, a  
 thin fluid jelly accumulates. This is noticeable in  
 figs. 16 & 17 beneath the right-hand mesenterial fila-  
 ment, and in figs. 44 & 45 at the angles of the oesoph-  
 agus. It is always to be found in the axis of the  
 young filaments, fig. 26. The distinction between  
 the supporting membrane and the more fluid  
 jelly, which is noticeable in larval stages, is lost  
 later in life. In the older larva, fig. 39 for instance,  
 the supporting membrane throughout its whole ex-  
 tent has become considerably thicker than in younger  
 stages, though the jelly in the axis of the filament,  
 fig. 35, is still to be distinguished from the more  
 membrane-like band of the mesentery. In the  
 adult the axial band of the mesentery is so much  
 wider, while the jelly in the axis of the filament  
 is at the same time denser, than in larval sta-  
 ges, that all distinction between the two struc-



eris is lost. Compared with an Actinia the whole mesodermic wall in the adult Maricaria is very scanty and membrane like, but in certain places it reaches a more generous, jelly-like condition, for example in the peripheral parts of the mesenteries as shown in fig. 57. Here the supporting substance is merely the thickened primitive membrane. Imagine it to get still thicker and at the same time more watery and you have the mesoderm jelly of an Actinia. Continue the accumulation of water, and you get the fluid and thick jelly of the Medusa umbrella.

There then seems to be no difference between the supporting membrane proper and the jelly, except in the more quantity of the secreted substance and in the percentage of water. What applies to the origin of one should explain the origin of the other. Now as regards the membrane proper, I am quite sure that in Maricaria at least it is formed as a cuticular secretion and not by the direct conversion of the ends of ectoderm cells into granular





matter which subsequently condenses as a membrane.  
 Turning now to the question as to which layer secretes  
 the membrane, we see from the figures (14, 17, 26, 45)  
 that after the mesenteries are formed, the lamella is  
 much more intimately connected with the endo-  
 derm than with the ectoderm: where the layers  
 are forced apart it always adheres to the endoderm.  
 But even here we notice that the ectoderm is pro-  
 vided with a well defined limiting membrane, which  
 is thinner than the lamella is essentially like it.  
 I conclude from this and other facts to follow, that  
 where the lamella lies between the two layers, both  
 layers share in secreting it. That the endoderm  
 cells can secrete the lamella, is plain, from its occur-  
 rence in the axis of the mesenteries, and in the axis  
 of the genital bands of a *Cubomedusa* &c. On the  
 other hand the same argument can be used to  
 prove the ability of the ectoderm cells to secrete  
 this substance, for in the column of *Hydromedusae*  
 there is a well developed lamella. In Perocentron?



I have pointed out that when the velum is developing the ectoderm cells range themselves so that their bases will secrete a continuous membrane.

### III. Formation of The First Pair of Mesenteries and Filaments.

III.

I was led to pay especial attention to the filaments by E. B. Wilson's interesting discovery that the dorsal pair of filaments in the Alcyonarian polyps are ectodermal lobes.<sup>(8)</sup> Like this pair, the filaments in general of Manicaria turned out to be lobes of ectoderm, which grow down from the oesophagus.

The oesophageal invagination in the earliest stages is symmetrically placed (figs. 4 & 5). It very soon however begins to travel towards one side of the larva. This is shown in the transverse section fig. 7, and still better in the longitudinal section fig. 6. (The endoderm in these two larvae is in different stages of development!). The lateral motion of the oesophagus has compressed the en-



ectoderm on its left into a compact mass, which completely fills the space between the oesophagus and body ectoderm. In the right hand the ectoderm has been stretched until it forms a single layer of cells. The narrow lumen of the oesophagus is filar, and its dilated extremity has no longer the symmetrical bulb like shape of fig. 5. In figure 8 the lateral movement has gone a step farther, and meanwhile the oesophagus has opened centrally. The movement of the oesophagus is continued until in one meridian there is nothing between the oesophageal and superficial ectoderm but the supporting lamella, figs. 11 & 12. (In fig. 11 the lamella has not yet appeared, but both stomodaeal and body ectoderm have smooth limiting surfaces). The intermediate stages show that the lateral movement of the oesophagus travels from above downwards, and that the ectoderm has consequently been pushed down in this meridian. This is proved by figs. 9 and 10, transverse sections from a larva



in which the oesophageal movement had gone further than in fig. 8. Fig. 9 is about at the level a in fig. 8, and fig. 10 is at the level b. In this larva then the oesophagus was closely pressed against the ectoderm at the level a, but was separated from it by endoderm at a lower level b. In the later stage fig. 11, the lowest part of the oesophagus has completed this journey. The meridian in which the oesophagus is thus pressed against the ectoderm, is that of the first mesentery. (Though figs. 9 + 10 are from the same larva, both the supporting lamella and endoderm are much further advanced in the lower section than in the upper!).

The larva from which the longitudinal sections, figs. 12 + 13, were cut, was very backward in forming the permanent endoderm. Fig. 12 is taken through the line a - b in fig. 11, and is in the plane of the first pair of mesenteries. It is only on the left side that the oesophageal ectoderm is in contact with the body ectoderm. But





The right side is evidently following suit, and in a slightly older stage (which I have not figured though I have a number of sections showing the point) is in the same manner closely pressed against the body ectoderm over a narrow meso-  
 Fig. 13 is to one side of a-b in fig. 11, and consequently is out of the plane of the mesenteries.

After the stage of which I have chosen in which both halves of the median longitudinal section are like the left half of fig. 12, comes the larva from which the series of transverse sections, figs. 14-17, was taken. It is this stage which clearly shows that the meridians, along which the oesophagus is pressed against the body ectoderm, are really then in the position of mesenteries. Fig. 14 is the uppermost of the series and is through the body of the oesophagus, the lower of which is immediately below. In the right side the oesophagus is separated by jelly alone from the superficial ectoderm. Following



down the series of sections, we see that in this meridian the oesophageal ectoderm sends down a slender lobe which, like the oesophagus above it, divides the endoderm and rests on an accumulation of jelly (right side of figs. 15-17). This lobe is a mesenterial filament. It is considerably shorter than the filament on the opposite side (fig. 17), and must therefore be the second one of the first pair. Thus the right side of the oesophagus in the larva is exactly in the condition shown in fig. 12 (left side), except that it has formed a filament.

On the left side of the larva (fig. 14) matters are more advanced. In comparing this side with fig. 12 (left), we see the oesophagus has moved away from the superficial ectoderm, but that while doing so has remained connected with it by a band of supporting lamella. Perhaps it would be more proper to say that the endoderm has grown in between the superficial and sub-surface ectoderm, and has thus wedged them



apart. On running through the series of sections, it is found that in this meridian also an ectoderm lobe has grown down from the esophagus. This lobe is the primary filament. It is much wider at its start near the esophagus than its fellow on the opposite side, but soon dwindles to about the same size. Like the esophagus above it, <sup>this filament</sup> it is in a more advanced condition than the filament on the right side. Since we know that the left side of the esophagus <sup>itself</sup> in this larva has passed through the condition which exists on the right side, we are pretty safe in believing that the ~~right~~ left filament has likewise passed through the condition in which the right filament is found. <sup>The</sup> ~~and~~ ~~latter~~ is a ~~early~~ <sup>near</sup> <sup>intermediate</sup> <sup>stage</sup> between fig. 12 (left) and <sup>this</sup> <sup>near</sup> <sup>staging</sup> larva, is to a certain extent supplied by the larva from which fig. 11 was taken. In this animal, which was sectioned transversely, the esophagus extended so much farther down in the meridian of the first mesentery than would its general size, that in this meridian it formed a





very evident though not a very long tube. This tube  
which, because the primary filament is shown in fig. 1,  
and is to be found in the three sections immediately  
below ~~at the base of the~~ <sup>the one figured</sup>, growing  
smaller towards its end.

On comparing the <sup>apparent</sup> first and second filaments  
in fig. 17, it becomes clear that the endoderm, which  
at a higher level grew in between the oesophagus  
and body ectoderm, has likewise forced its way  
beneath the primary filament, and thus given rise  
to the first mesentery. The mesentery is continued  
from the level of fig. 17 downwards, as a very slight  
endodermic ridge on which rests the filament.  
The axial band of suspensory lamella (fig. 17) is  
seen to be continuous with a thinner lamella sepa-  
rating the filament from the endoderm. Imme-  
diately beneath the opening of the oesophagus the  
mesentery is much more elevated than at a  
lower level. The elevation of the mesentery in this  
region is connected with the first appearance



of an intramural chamber.

In the loma which we have been studying the first pair of intramural chambers has been marked off. Round the oesophagus however they are still solid (fig. 14), though at a lower level the hollowing out of the solid endoderm has begun. At this level, fig. 5, which is just beneath the opening of the oesophagus, the endoderm on one side of the first mesenteric insertion <sup>the cavity when</sup> contains a small cavity <sup>which</sup> ~~which~~ <sup>is</sup> faced through the series of sections is found to open into the general gastric cavity <sup>(fig. 16)</sup>, forming as it does so the core or bay which underlies and has the primary bilayers in it. This figure 20 is then comp. figs. 4 + 5! is the larger of the two primary chambers that the excavation of the solid endoderm begins. Indeed, as I show from other series of sections, the excavation of this chamber is nearly completed, before that of the smaller begins. The excavation starts, as we have just seen, in the immediate neighborhood of the first mesenteric. From



This spot it gradually extends across the chamber to the second mesentery, reaching all the while from the tip of the oesophagus upwards.

Let us now return for a moment to the second mesentery. This which exists in its embryonic condition in fig. 14, soon shows the growth of the primary mesentery. In figure 18 it is completely formed, and in the series of longitudinal sections figs. 20-23, which I shall describe farther on, the second mesentery is in the condition in which the primary mesentery of fig. 14 is found: i.e. in its neighborhood the larger of the two intramural chambers is solid, while the smaller chamber is entirely solid.

In the larva in which the transverse section fig. 18 was made, the various processes which have been described are <sup>now</sup> completed. The oesophagus is passing by its complete mesenteries. Both intramural chambers the larger on the left, the smaller on the right, have been hollowed out. Below the oesophagus the mesen-



ine ridges extend the whole length of the larva, and the first pair of filaments about half the length. The section is slightly complicated by other features which I shall now discuss.

In the larger 1. the two chambers (fig. 18) the second pair is mesenteric  $\underline{3} + \underline{4}$  has appeared. The axial bands in the lamella as yet cause no appreciable elevation of the endoderm, and at a level slightly below the oesophagus are entirely lost. In fig. 18a, a section above fig. 18, the axial band numbered  $\underline{4}$  stretches across to the oesophagus, and still higher up  $\underline{3}$  does likewise. In this section the position of the oesophagus is seen to be asymmetrical. This is almost always the case at the extreme upper limit (the appearance is not due to oblique sections), and hence one mesentery usually runs out before its fellow ( $\underline{2}$  before  $\underline{1}$ ). The mode of origin of the second pair of mesenteries is thus entirely different from that of the first. All the subsequent mesenteries are formed after the fashion of the





second pair.

Looking again at fig. 8 we see that while the outer wall of the larger chamber is made up of unmistakable endoderm, the inner or oesophageal wall has an epithelium precisely like that of the oesophagus. Both are made up of very slender elongated cells, which when isolated are found to be more or less spindle shaped: The nucleus causes a thickening in the cell, from which run a central and peripheral process; the peripheral end is enlarged and flattened so that by the juxtaposition of many such cells, a continuous cuticle can be formed. In a word the cells in question are the well-known "supporting cells" of the Hertwigs (9). Besides the supporting cells glandular cells are found. These are slender cells filled with granules which stain intensely with haematoxylin. Nervous elements may be present, but I could not distinguish any. The epithelium of the oesophageal wall of this chamber is moreover sharply marked off from the



rest of the epithelium. It is directly continuous with the oesophageal ectoderm round the lip of the oesophagus, and is evidently a part of ectoderm. Any doubt which might cloud this point is effectually removed by later stages such as figs. 44 + 45, where the epithelium which is claimed is ectoderm actually overlaps, at its upper limit, the endoderm. It is clear that in this stage the oesophageal ectoderm has been reflected round that portion of the lip (the edge of oesophagus) which belongs to the larger chamber, and has then run up along the outer side of the oesophageal tube, covering the endoderm before it. The direction of growth is reversed, but otherwise the ectoderm is acting in precisely the way which it does in forming the first pair of elements. In the smaller chamber is fig. 8. The epithelium forming the oesophageal wall does not differ from the rest of the endoderm. In a later stage when the third pair of mesenteries has appeared, the



ectoderm is also reflected round the lip belonging to this chamber, and runs up along the oesophageal wall (figs. 36 + 39).

The reflection of ectoderm which leads to the condition shown in fig. 8, commences as soon as the excavation of the primary (larger) chamber begins, and follows close on the heels of the latter process. The object of the reflected ectoderm, as will be shown later, is to provide filaments for the young mesenteries before the latter are complete; i.e. continuous from body wall to oesophagus. Bearing this in mind it is probable that the reason why the ectoderm is reflected into the larger chamber at such an early date, is that the second pair of mesenteries will be formed in this chamber. The series of longitudinal sections figs 20-23 illustrates the early reflection of ectoderm round the lip of the larger chamber. The larva from which this series was made, was at a stage intermediate between figs. 14 and 18. The supporting lamellae of both



mesenteries were complete, as in fig. 18, but the inter-  
mesenterial chambers were far from perfect. The  
smaller chamber was entirely solid, and the cavity  
of the larger was not entirely excavated. In spite of  
the difference in age, it will do to refer the planes  
of the longitudinal sections to fig. 8. The section  
fig. 20 thus is taken through the mesenteries 1 + 2  
and the corresponding filaments. The next three  
figures represent consecutive sections to the left of  
this plane, the one farthest to the left lying in  
the plane a-b of fig. 18. Finally the left hand  
mesentery in fig. 20 is the primary mesentery, 1 in  
fig. 8. With this orientation it is seen on glancing  
through the series 20-23, that only in the neigh-  
borhood of the primary mesentery has the chamber  
been hollowed out: in all the sections the endo-  
dema is solid on the right side of the mesenteries.  
From the sections after fig. 23 I learn that about  
one half of the chamber has been excavated. Now  
in fig. 23 the <sup>mesenterial</sup> ~~endodema~~ chamber is the left of the





embryonic) is in the state in which it has been found:  
 The ectoderm has not yet been reflected round the  
 peripheral lip. But in the sections nearer to the  
 mesoderm, figs. 22 & 2, the ectoderm has been  
 reflected and has driven the endoderm before  
 it. The reflection of ectoderm, as I have said,  
 follows very closely the excavation of the chamber.  
 As the latter proceeds from mesoderm to mesoderm  
 2 (fig. 18), so does the former; and by the time the  
 chamber is completely established, the ectoderm  
 is reflected all the way from 1 to 2, as is  
 seen in fig. 18.

In the larva which was used to illustrate  
 the earlier appearance of the primary intra-  
 vidual chamber, figs. 4-5, the reflection of ecto-  
 derm had already begun in this place, round  
 one edge of the primary peripheral lobe (fig. 4,  
 left!).

To sum up the more important events described  
 in this section:



To form the first mesentery the whole oesophagus moves laterally, until in the meridian of the mesentery there is only a supporting lamella between the oesophagus and superficial ectoderm. The oesophagus now grows downward in this meridian as a lobe of ectoderm which represents the primary filament; and which passes the esophagus before it. On the opposite side of the animal, along the line of the second mesentery, the oesophagus becomes applied to the body ectoderm in the same manner, and a lobe grows down from it to form the second filament. The mesenteries as such are formed by the ingrowth of the ectoderm between the body ectoderm and oesophagus above, and between the body ectoderm and filaments below. The primary <sup>visceral</sup> mesenterial chambers are at first solid. The large chamber acquires its cavity before the smaller, the excavation travelling from the lip of the oesophagus upward, and from the first toward the second mesentery. The excavation of the primary



chamber is closely followed by the reflection of ecto-  
derm into this chamber, the reflected ectoderm  
running up the respiratory wall and covering the  
endoderm before it. The second pair of vesicles  
appear in the larger chamber as longitudinal ridges  
of the supporting lamella, which cause no ele-  
vation of the endoderm.

#### IV. Histology of the Larva.

IV.

It may now be advisable to describe the histolo-  
gy of the larva, going where necessary beyond  
the stages already studied.

##### a. The Surface Ectoderm.

The ectoderm at the time when the supporting la-  
mella is formed, figs. 5+6, consists of columnar  
cells, the protoplasm of which shows a great ten-  
dency to break into small polygonal balls. When  
the ectoderm is in this condition the <sup>mucous</sup> ~~mucous~~ cells  
appear (figs. 6, m, figs. 7, 8 etc) as pear shaped  
bodies in the peripheral ends of the columnar cells.  
The contents of the pear shaped body stains a deep



blue with leucotrylin, and is thus distinctly marked  
off from the surrounding cells. It appears to be  
shed from the start, as even in such young stages  
as fig. 7 many of the mucous cells have poured  
out their contents, which adheres to the mouth of  
the cell as a little mass of a deep blue color. The  
tendency of the mucous cells to eject their contents,  
presumably when the ecdysis fluid touches the  
larva, is very noticeable in older stages such as  
fig. 27, which are often completely covered by a thin  
layer of mucus. The mucous cells increase in size  
and number, until they become the prominent  
feature of the ectoderm (figs. 19, 20, 21). In their  
final condition, fig. 27, they are large clear sacs  
in which a few strands of intestine may be  
seen in carefully prepared osmic specimens. The  
nucleus of the original cell, in which the sac de-  
veloped, can not be made out in sections.

The mucous cells develop over the general  
surface of the larva, but are not found at





The aboral end. Here their place is taken by a slender elongated cell full of granules, which stain even deeper with tannin than the mucous cell. The granular gland cell is early recognized in its earliest stage, and is formed from the embryonic ectoderm cell by a deposition of granules throughout the length of the cell. The granular cells though especially grouped at the aboral end of the larva, are found here and there over the general surface.

The remaining cells of the embryonic ectoderm become for the most part transformed into spindle shaped "supporting cells", which I have already described in dealing with the reflected ectoderm. Thread cells, n.c., ~~fig. 14~~, are first noticed in larvae at about the stage of fig. 4. Whether the ectoderm forms any muscle cells I do not know. The larvae can alter their shape to a great extent, but the fibres are probably all endodermic.

Study of -

For the nervous elements Narcissus are all



stages is a very unsatisfactory subject. Even the  
gorgonian cells which show so plainly in sections of  
Actinian larvae, I was not able to make out in the  
coral. There is however a finely granular granulation at  
the base of the ectoderm, which is very thin over  
the general surface, fig. 26, but at the alveolar end  
of the swimming larva is thick and easily seen,  
fig. 20. When the living larva is compressed, this  
accumulation of granular substance is very mani-  
fest. It is perfectly clear, and until I began to  
section I thought it was jelly. When carefully  
examined the granular layer in this region is  
found to consist of a mass of fine ~~granular~~ <sup>sub-</sup>micro. It  
is very probably nervous. The fact that the Cere-  
brated planula in general moves with its alveolar  
end in front, taken together with the occurrence  
of a bunch of long cilia at this end in many Ac-  
tinian larvae, suggests the existence of some  
most primitive nervous centre as I take this ac-  
cumulation of granular matter to be.



When the various elements of the ectoderm have been completely differentiated, fig. 26 (from a stage a trifle older than fig. 29), a finely striated cuticle is secreted. In all respects this cuticle is described by the Hertwigs for *Aetideas* (9. Taf. III). The cilia with which the <sup>body</sup> ectoderm is completely covered, and with which the oesophagus and filaments are likewise provided, I have not represented in the figures.

#### b. Oesophagus and Filaments.

The oesophagus and young filaments, fig. 20, have the same structure as the superficial ectoderm, except that mucus cells are absent, and granular gland cells are more abundant than over the general surface. As a rule it is only in the youngest stages that the reflected ectoderm (fig. 18) contains gland cells, and even then they are scanty. In later stages, fig. 24, mucus cells are found in the upper part of the oesophagus immediately round the mouth, and very large thread cells,



figs. 24 & 27, appear in considerable numbers in the outermost epithelium, extending down into the filaments. The histology of the filaments will be treated in detail in a later section.

### C. Endoderm

The endoderm after its first invagination remains about the same through the larval life. I am not sure whether it is ciliated. The cells are cubical or columnar, and contain one or more large and distinct vacuoles. The peritelson is granular and rather coarsely reticular. The cell outlines can only be made out with a little care. The number of yellow cells steadily increases with age. A few very fine muscle fibres can be made out here and there, especially in the mesenteries, and a more or less continuous layer probably exists.

In doing, the general similarity between the endoderm of the coral larva (practically the same in the adult *Manicina*) and the Ac-





linear ectoderm as described by the Hertwigs, may be noticed. In particular the two kinds of gland cells in the Actinias are exactly represented in the coral. The Hertwigs suggested that ~~probably~~ possibly the granular gland cell was but a stage in the development of the mucous cell, but this appears not to be the case as the two are easily distinguished from the start, and have also a different distribution.

V. Mesenteries and Filaments from the  
Second to Sixth Pair.

V.

Before proceeding to the detailed <sup>description</sup> ~~account~~ of the reflection of ectoderm, which as I conclude leads to the formation of all the filaments except the first pair, it will be convenient to give a brief account of the order in which the mesenteries appear.

The first appearance of the second pair of mesenteries has already been described, (fig. 5. In fig. 27, trans. sec.) a later stage. This pair is complete at the level of



is the figure. At a lower level, just above the tip, fig. 28, while one of the pair 3 is still complete, 4 is incomplete (the section is slightly oblique). This difference in growth between the two members of the second pair is an exception: They usually develop at the same rate. Below the oesophagus, fig. 29, both members exist as slight ridges which extend the length of the larva.

The third pair of members has appeared in fig. 27. They remain insignificant during the swimming life of the larva. After the larva has become attached, the third pair is prominent, and the fourth pair is also ~~the~~ found in the position shown in fig. 3 - (naso. sec. taken below oesophagus - The primary members are supplied with large and coiled elements). According to Lacaze Duthiers the fourth pair appears between the first and second pairs. The Herwig suggests (9) on general grounds of symmetry that the order of appearance was as I have figured. As n.



gives the fifth and sixth pairs however, the old account of Lacaze Duthiers holds for Manicaria as against the figures given by the Sterlings for Adamsia (9- Taf. 1, f. 3). This is seen in representing fig. 39, a transverse section through the oesophagus of a stage with three mesenteries. The fifth and sixth pairs develop unilaterally on opposite sides of the primary mesenteries. In Adamsia according to the Sterlings, the two pairs of mesenteries appear on opposite sides of the long axis of the oesophagus, in the chamber between the first and second pairs.

As fig. 39 represents my oldest larval stage I was not able to trace the development of the muscle plates and consequent rearrangement of the four ~~two~~ primary mesenteries. According to the accepted account the pairs 3 & 4 in fig. 39 become the diaphragm pairs, and on each side of the long axis of the oesophagus 5 & 1 unite to form one pair, and 6 & 2 another pair.



In this connection it may be observed that after the larvae became attached, the lumen of the oesophagus appeared decidedly bilateral in the living animal, and took the relations to the mesenteries shown in fig. 39. The shape of the lumen is however susceptible of great changes, and in many of the sections through attached larvae the typical shape is not retained, fig. 30, or the oesophagus is compressed in the long axis and drawn out in the short, fig. 45. In the swimming larva the small size of the mass will not permit one to decide as to the shape of the oesophagus from surface views. After examining a large number of sections I conclude that in stages as old as fig. 27, the ~~lumen~~ arrangements are as in the attached larva: the lumen is bilateral, and has one of the first pair of mesenteries on each side of its long axis. As regards earlier stages, such as figs. 7, 14, 18, I could not decide whether the oesophagus had acquired its bilateral character.





We now come to the formation of filaments for the second and subsequent pairs of mesenteries. In fig. 18 the reflected ectoderm which forms the oesophageal wall in the larger chamber extends horizontally from 1 to 2. The mesenteries 1. the second pair 3 & 4 are extremely incomplete. In fig. 27 these mesenteries are complete, and now the reflected ectoderm does not extend from 1 to 2, but is represented by the patch R E, between 3 & 4. In sections of the same larva (figs. 28 & 29, below the level of fig. 27, a certain irregularity marks its appearance, which is connected with the formation of the third mesentery and so, which I shall discuss later on. In the typical larvae of this stage the sections below fig. 27, between it and the lip of the oesophagus, are precisely like fig. 27. This means that the mesenteries 3 & 4 are both complete throughout the length of the oesophagus, and that the oesophageal wall in the chambers enclosed between 2 & 3, and 3 & 4, re-



structure is endodermic. At the very top of the  
 oesophagus in some larvae, the oesophageal walls  
 & these chambers are ectodermic. In a section  
 just below the oesophagus it is found that the  
 mesenteries 3 & 4 have short filaments. Further  
 the tract of ectoderm R.E. only extends up-  
 ward for about one third the length of the oesoph-  
 agus. It will be remembered that in the stage fig. 18  
 the reflected ectoderm extends nearly the whole  
 length of the oesophagus. Now what has taken place  
 in the transition from the stage fig. 18, into the  
 stage fig. 27? Plainly it is that the mesenteries 3 & 4  
 as they grew <sup>down</sup> ~~down~~ and gradually became em-  
 pleti, carried along with them the reflected ecto-  
 derm, part of which came to lie along the mesen-  
 teries as short filaments, while the remainder  
 was divided into three portions. Of these por-  
 tions the two lateral, those which originally  
 extended from 2 to 4 in the one row, and from  
1 to 3 in the other - fig. 27, were carried all the



way down to the tip of the oesophagus, while the middle portion EE was not carried the whole way down. It is of course possible and on more accounts probable that the tract EE was like the rest of the original tract, forced down to the tip, but that later it grew up again.

A couple of longitudinal sections will further elucidate the series of changes which separate fig. 8 from fig. 27. The sections given in fig. 25 were made from a larva at about the same stage as fig. 27. The two mesenteries of the first pair had filaments which extended the length of the larva, and the mesenteries of the second pair were complete and equally advanced. The section b in fig. 25 is a radial section through one of the second pair of mesenteries, say b in fig. 27. The mesentery is complete, and its edge clings a short filament. The other mesentery of the second pair with its filament, is the exact counterpart of the one shown. In cutting the larva which ex-



actly radial sections of one mesenteric were obtained, equally true transverse sections were made of the other. The precisely horizontal plane in which the filaments of b lie, is probably due to the undulatory motion of the larva, on being sealed, in the direction of the shorter transverse axis of the amphagus (The transverse section would be elongated in just the a direction at right angles to the long axis of fig. 27). The section c in the same figure (round in the figure so as to complete the oesophageal lumen) is the second section to one side of b, and a is the second or third on the other side. Comparing all three figures with fig. 27, b is through mesenteric 4, a is on the far side of 4 and consequently cuts the reflected ectoderm R.E., c is on the near side of 4 and the ectoderm is not reflected round the free edge of the oesophagus.

Figure 24 is a single longitudinal section from a stage slightly older than the one just described. On the right it is through one of the second pair of filaments, and on the left





through an invagination chamber. Referring the section to fig. 27, the right half is through mesenteric 4, and the left through the chamber opposite, at about the point x.

Having now described the ordinary way in which the first and second pairs of mesenteries and filaments are formed, I will take up an exception, which as we shall see later has some bearing on the relationship between the *Enthemon* and *Scyphos medusae*. Figs. 30-33 are transverse sections run from above down, of a larva in which the first pair of filaments extended about  $\frac{1}{2}$  the length of the body. The outstages throughout its vertical extent is apposed to the superficial ectoderm over a wide tract, a to b in fig. 30. On running through the series of sections it becomes evident that the tract a - b is not the mesenteric of a single mesentery, as it would be in a normal larva like fig. 27, but is the space between two mesenteries. The first section below



The embryo, fig. 3, shows that a rather wide lobe of ectoderm is growing down, and also that between a + b. This lobe has been forced apart from the body ectoderm. In fig. 32 two sections marked between 3 + 32 a lobe of endoderm has grown in between a + b, and has thus given rise to two mesenteries, which are provided with a common filament. In the section below, fig. 33, the lobe of endoderm has been folded out, and the two mesenteries definitely established. In a section (not figured) below fig. 33, the mesenteries a + b exist as separate ridges, and the common filament has split into its constituent parts, 1 + 3. The filament 3 extends a very short distance down, and the mesentery b only reaches the equator of the larva. The mesentery a with its filament is the fellow of 2 in the present case as fig. 32. The two mesenteries belong to the first pair. I have assumed that a is the minor mesentery since its filament is longer than that of 2.



Bearing in mind the normal development as illustrated in figs. 12 and 14, the exceptional character of this larva is due to the fact that one of the second pair of mesenteries is formed at the same time and in the same manner as the mesenteries of the first pair. This abnormal member of the second pair, b fig. 30 re., may be called the third mesentery. We may suppose that the mesogaster, applying itself to the body ectoderm along the line not only of the first <sup>a</sup>, but also of the third mesentery, b, was unable to force down the ectoderm in these lines without coming down at the same time the ectoderm between a and b. Thus arose the condition shown in figs. 30 & 31. When the time came for the mesenteries as such to be formed, the ectoderm which had been pushed down between a & b was compelled to grow up again, becoming excavated so as to form the intermesenterial chamber. It is in this process that we see the ectoderm in figs. 32 & 33.



The irregularity of the larva it will be noticed is confined to one side side: The right side of the sections is normal, and no doubt the other member of the second pair of mesenteries would have developed in the usual way.

The larva just-described was the only young specimen I observed, which exhibited this peculiar variation. I found a few older individuals however in which one of the filaments of the first pair was so intimately connected with one of the second pair, as to render it probable that the two were simultaneously formed from a common lobe in the manner shown in figs. 30-33. The larva, figs. 27-29, to which I have already referred several times, comes under this head. Though the section, fig. 29, is at an appreciable distance below the oesophagus, the filaments 1 & 3 are still united, and bear evidence to their common origin. The other member of the second pair, 4 in fig. 28, has itself been





formed, and is gaining its filament, in the normal manner. The reflected ectoderm only extends from 2 to 3, and if the latter mesentery has been formed in the manner suggested, the ectoderm never was reflected between 3 & 1.

Returning to the normal development we have now to trace the origin of the filaments in the third pair of mesenteries. These filaments are derived from a lobe of ectoderm which is reflected into the wall of the two primary chambers. The reflection takes place after the larval lobe become attached. In a stage with twelve mesenteries, fig 39, the lobe is marked X. The section is taken at a level higher than that reached by the lobe belonging to the chamber c (compare R.E. in fig. 27). In a section just above fig. 39 the third pair of mesenteries bury themselves in the lobe X, much as 4 does in fig. 28. In the uppermost sections where the mesenteries are complete, X is not found. After a great many



trals I succeeded in getting a radial section  
 through one of the pair of membranes, which had  
 forced down the reflected ectoderm so that the  
 latter lay along its free edge as a tiny fila-  
 ment; fig. 38 left half (right half is through chamber  $\epsilon$   
 of fig. 39). The lobe for the third pair of fila-  
 ments is almost always present in larva with  
 eight membranes: in fig. 36, a section just above  
 the lip, it is marked  $\epsilon$ . In this larva the  
 membranes of the second pair are backward in  
 development; they are not yet perfectly complete,  
 though on one of them a very small filament  
 is seen.

As the fourth pair of membranes continue  
 to increase in size the lobe of ectoderm which  
 belongs to the chamber  $\epsilon$  in fig. 39, extends farther  
 upwards. In fig. 39 it reaches about the same  
 level as in fig. 27 (R.E.). In a slightly more  
 advanced stage, fig. 38 (right half), it extends  
 nearly the whole length of the oesophagus; and in



the series of transverse sections, figs. 43 + 45, is dis-  
 sected extends to nearly the uppermost limit of the  
 chamber. The latter series is a very good one as  
 the polyp was killed in its natural shape. In life  
 when the young coral is expanded, there is a very  
 distinct oral cone, indicated by the line m-m  
 in fig. 38. In drying the oral surface is almost always  
 retracted, and the median longitudinal section  
 is then as in figs. 37 + 38. The transverse section  
 fig. 43 is taken through the line x-y in fig. 38. Figs.  
 44 + 45 lie above it. In the larva from which the  
 series was made, both the third and fourth pairs  
 of tentacles were very well developed below  
 the level of x-y (fig. 38), but above this line  
 they were not perceptible. Judging from all  
 my other sections I should say that this rapid  
 development of the tentacles along the side wall  
 of the polyp, as contrasted with their back-  
 wardness in the upper oropharyngeal region, was  
 exceptional. In the sections the first and se-



and pairs of mentories are complete. The chambers a + b together with c represent the larger of the two primary chambers. The walls of a + b are endodermic except for a short distance above the oesophageal lip, but in c and d (the smaller of the two primary chambers, the reflected ectoderm extends very far up. As the third pair of mentories lie in chamber d, the ectoderm of this chamber, as might be expected, extends farther up than in c, in which lie the fourth pair. In the ectoderm of d there are a few large nettle cells, a rare occurrence. At the upper limit of each tract of ectoderm, the overlapping of the layers previously referred to, is clearly shown. This overlapping of the layers which is common is noticed in a good many specimens. In fig. 37, the left half of the section, through an intermentorial chamber, exhibits this phenomenon. The right half of the section is through one of the second pair of mentories.

The fifth and sixth pairs of mentories





appear simultaneously, but it is convenient to speak of one pair as the fifth, and the other as the sixth. They are still very small in my oldest larval stage. The filaments for the fifth pair are probably formed from the lateral portions of the lobe x (fig. 39), after it has been divided by the completion of the third pair of mentories. The filaments for the sixth pair it seems will be formed from the tracks of ectoderm which belong to the chambers a + c (fig. 39). These tracks it will be remembered were in most larvae pushed completely back to the free edge of the oesophagus, when the second pair of mentories became complete. In stages with twelve mentories however, such as fig. 39, they have again appeared, though they usually extend but a very short distance above the lips. In a couple of larvae as old as fig. 39, they were unusually well developed, reaching as far up as the track for chamber c.

In summing up the facts of the ectoderm re-



Median, it will be convenient to refer to fig. 39. The ectoderm, which is reflected into the lumen of the two primary chambers, is again pushed down by the growth of the second pair of mesenteries. From it are formed the filaments for these mesenteries, while the remainder of the original tract splits into three divisions. The middle division, chamber c, is not pushed entirely to the edge of the mesophares; late in life when the fourth pair of mesenteries is well developed, it grows once more nearly to the upper limit of the mesophares. The lateral divisions a + b are pushed to the edge, but after the sixth pair of mesenteries has appeared, they begin to grow up again. When the mesenteries of the third pair are well advanced the ectoderm is reflected into the walls of the two primary chambers, and runs up the oesophageal wall nearly to the top of the chamber. The mesenteries, when they begin to grow down, carry a part of the ectoderm along their inner edges as very slender



filaments. The growth of the various *ectoderm* reflected ectoderm is thus seen to follow in general the order of development of the mesenteries.

## V/. Filaments of the Adult.

V/.

After studying the larval development it seems very sure that the filaments of the first twelve mesenteries are *ectodermal*. Further I think the stage with twelve mesenteries holds the key to the condition in the adult. In this stage we have complete (first and second pairs) and incomplete mesenteries (third pair), both provided with *ectodermal* filaments. Both kinds of mesenteries are exactly comparable with the two kinds in the adult, and if the incomplete mesenteries of the larva are successively supplied with filaments by the reflection and upward growth of the *ectoderm*, it seems probable that the incomplete mesenteries of the adult are supplied in the same manner.

The gap between my series of larval stages and the adult is partially indicated by the



transverse sections, figs. 41 & 42. The young <sup>manicera</sup> ~~coral~~ from which these sections were made was  $\frac{1}{8}$  in. diam. I found a couple of about the same size on a piece of coral rock. Fig. 41 is through the oesophagus, and disregarding the skeleton, shows six pairs of complete and six pairs of incomplete mesenteries. The twelve complete mesenteries represent the mesenteries present in the larva (fig. 39), now rearranged in two and with simple muscle plates (only shown on the distinctive mesenteries). The incomplete mesenteries have appeared according to the general law governing the mesenteries above twelve.

Manicera remains a single polyp until it has reached a diameter of something less than half an inch. In this condition it is disk shaped, and has the character of the adults, except that dependent on asexual multiplication. It is moreover not sexually mature. Such a coral has, disregarding local irregularities, twelve pairs of mesenteries of the first order (complete), twelve of the second order (incomplete), and





twenty four joins of the third order (much were incomplete).  
 Fig. 50 gives a median longitudinal section of the coral at  
 this age. The polyp was in a state of complete contrac-  
 tion, the oral surface or peristome Pr pulled down, the  
 mouth Mo widely open, and the tentacles T retracted.  
 The section on the right is through a mesentery of the  
 first order, on the left through one of the second order.  
 In each side, the mesentery is divided into a central  
 and peripheral part (R.P.) by the calcareous theca.  
 When the animal is expanded, the peristome is lifted  
 high above the level of the mesenteries. It then embraces  
 the whole width of the animal, the tentacles forming  
 a dense ring round its edge, while the mouth is  
 narrowed to a slit-like opening.

On the right side of fig. 50 the epithelium of  
 the oesophagus, Oe., is directly continuous with the  
 pharynx, the mesentery being evident. On the left  
 side, the mesentery being mesenteric, the oesophagus  
 has a free edge. Now if my view is correct, not only  
 the living epithelium of the oesophagus is certain.



mal, but the epithelium X, which forms the gastric covering of the oesophagus and peristome, is likewise ectodermal: The ectoderm here as in the larva is reflected round the lip of the oesophagus and extends upwards until it reaches the secondary mesenteries, down which it courses as the filaments. Fig. 55 is a more highly magnified view of the lower part of the oesophagus as shown in the left half of fig. 50. The living epithelium of this part of the oesophagus (the lower third) is composed of slender spindle shaped cells. The upper two thirds contain large nettle cells, and in the region of the mouth mucus cells. The epithelium on the outer <sup>superior</sup> side of the oesophagus is for some distance (compare fig. 55 with fig. 50) exactly like the living epithelium, except that it contains a few yellow cells. Then comes a region of vacuolated cells, which is followed by a very low epithelium made up of exceedingly small cells, the exact shape of which I could not determine. The low epithelium is continued



up the oesophagus and over the peristome, and is continuous with the filaments on the secondary mesenteries. These filaments though of large size at a lower level, gradually become very small as they approach their upper limit, and by this means run without any trace into the low epithelium covering the peristome. It will be remembered of the larva that the filaments on the third pair of mesenteries were likewise very small in the upper part of their course, though to be sure in my oldest stage they <sup>as yet</sup> ~~grey~~ existed in this part (figs. 36 & 38).

The view that the gastric lining of the oesophagus and peristome is ectoderm, can only be held by supposing the epithelium in question to have suffered a ~~great~~ <sup>great</sup> histological change. It is possible that a very careful histological examination of the epithelium would show that it does not differ so much from the ectoderm, as appears to be the case. But though this kind of epithelium can not be said to resemble the ectoderm, it differs quite as



much from the undoubted endoderm. The endoderm of the adult (figs. 51 & 52) is made up of large irregular columnar cells packed with "vacuole cells", the vacuoles present in the larval endoderm being confined to special localities. The only apparent alternation in the view offered, is that while the first twelve mesenteries are provided with ectodermal filaments, <sup>the filaments of</sup> all subsequent mesenteries are endodermal. <sup>since</sup> As the several orders of filaments in the adult differ only as regards size, and since even this difference is obliterated by the constant transformation of incomplete into complete mesenteries during the growth of the coral, it seems improbable that such precisely similar organs should be made by both layers.

On the other hand E. B. Wilson (8) came to the conclusion that the dorsal pair of filaments in the *Alcyonaria* were ectodermal lobes, but that the remaining six filaments were purely endodermal. The two kinds of filaments in these polyps have however a very different differ-





histological structure, with which is associated a division of color.

Von Steiner (11) several years ago decided that the filaments of Cerianthus were ectodermal. He reached his decision by a histological study of the adults, and though this method is inconclusive, I am not surprised, after studying myself some immature specimens of Cerianthus, that he came to this view. The writings in their classical work on the Aequorea pointed out that embryological deductions based on adult histology are not very reliable, and also brought forward as an objection to Von Steiner's view, the existence of filaments in the Aequorea generally in incomplete mesenteries.

## VII. Histological Structure of the Filaments.

VII.

The very young filament is shown in cross section in fig. 17. In this larva the first pair of filaments extend about half the length of the body. In fig. 29 though the mesentery is elevated above the general ectoderm, the filament retains its simple character. It is roughly hemispherical



in section and is separated from the mesentery by a thin sheet of supporting membrane. Besides supporting cells the filament contains granular gland cells. In most larvae in which the first pair of filaments reach the aboral end of the body, the filament is no longer separated from the mesentery by supporting lamellae. Fig. 25 gives a surface view of such a larva, and fig. 26 a cross section of one of the long filaments. In the latter figure the sheet of supporting lamellae on which the filament formerly rested, has given place to an accumulation of jelly at the apex of the mesentery. Though the cells of the filament are practically continuous with this gelatinous axis with the cells of the mesentery, the line of demarcation is very evident on each side owing to the different histological characters of the endodermal and filament cells. In the filament there are now numbers of large nodule cells, and the gland cells are far more numerous than in earlier stages. Nervous elements are very probably present as there is a granular condition in the deepest part of the filament. It is seen



from fig. 9 The filaments increase in size towards the lower end. Towards the end of the swimming leg the first pair of filaments begin to get slightly curved and twisted in the lower part of their course.

Fig 35 is through one of the first pair of filaments, and its mesentery, of an attached larva with eight mesenteries. In the attached larva these filaments pursue a straight course for a short distance below the oesophagus. In the lower part of their course, they are curved and twisted as in the adults, and in this region sections like fig 34 are got. Fig. 35 is through the straight portion of the filament. In comparing this again with fig. 20 (magnified to same degree) it is seen that the mesentery has become more elevated and at the same time thinner, also that where the endoderm cells end and the filament cells begin there has been a pinching in, which added to the actual bulging out of the filament has very distinctly marked off the latter from the mesentery. The bulging out of the filament is due to the lateral expansion of the



anal jelly shown in fig. 26. The extension of the jelly has  
 no lower place than the filament, fig. 35, is divided  
 into three portions: the main body, in which are  
 contained the nettle and gland cells; and two tracts,  
v. l., which may be called the ventro-lateral tracts. The  
 latter are made up exclusively of slender supporting  
 cells. As in the swimming larva, the filament cells are  
 sharply marked off from the cells of the mesentery. In spite  
 of the twisted condition of the lower part of the fila-  
 ment, sections show that the structure is the same  
 as in the upper portion.

In the adult the upper portion of the fila-  
 ment or a complete mesentery is comparatively straight;  
 but the main portion is twisted, fig. 50. The fila-  
 ments of the incomplete are considerably less twisted  
 than those of the complete mesenteries. The filaments  
 are attached their whole length to the mesenteries,  
 there being no free acanthopores; they are however  
 capable of extension, both through the mouth and through  
 I could not find the opening through pores in the





lateral body wall. Unlike the larval filament, that of the adult has a different structure in its different portions. Figs. 52, 53, & 54, are sections through the different parts of a filament in a complete mesenteric.

Fig. 52 is through the upper third. The filament itself has almost exactly the shape shown in fig. 35, but the mesenteric has become swollen out so as to form two lateral lobes, m. l., between which the filament rests. The veris. lat. tracts are much better marked in the adult than in the larval filament. This is due to the continuation of the pinching in process, which had already gone some distance in fig. 35, and to the outgrowth of the mesenteric lobes. By these two means the slender "waist" is produced, which indicates the separation of filament and mesenteric.

The veris. lat. tracts of the filament both in the upper portion of its course, fig. 52, and lower down, figs. 53 & 54, are made up exclusively of supporting cells. The main body of the filament in fig. 52 contains a large number of granular gland cells



and numerous nettle cells. The mesenterial lobes are composed of cells which do not differ essentially from the rest of the endoderm. They are only much elongated and contain a number of very large vacuoles. The passage of the filament into the oesophageal epithelium is effected in the following manner: Immediately below the oesophagus the "waist" in fig. 52 becomes gradually wider until the ventro-lateral tracts no longer exist, and the filament cells are continuous with the mesenteric cells round the horns, h, of the supporting lamella of the filament. By this time the filament or oesophageal lobe is much flatter and wider than in fig. 52, and the supporting lamella of the filament is also nearly flat. The latter passes directly into the supporting lamella of the oesophagus, and the filament into the lining epithelium of the oesophagus.

Fig. 53 is through the middle third of the filament. The gland cells are absent in this region, but the nettle cells are very large and exceedingly abundant. The mesenterial lobes are not so well



developed as in the region above.

The lower third of the filament, fig. 52, contains neither nettle cells nor the typical gland-cells. The body of the filament is here made up of very large granular cells between which are scattered a few supporting cells. The granules are much more numerous in the peripheral than in the central parts of the large cells, <sup>and</sup> on the sides of the filament where the main body passes into the ventrolateral bracts, they become gradually restricted to the peripheral ends of the cells. The granules are chemically different from those in the ordinary granular gland cell. They do not stain especially well with hematoxylin, but become dark brown with osmic acid. In a number of filaments these peculiar granular cells contained large angular cocrystallizations, which stained dark red with eosin carmalum, while the cell body takes the stain but faintly. The mesenterial lobes in this region are slightly less pronounced than in the immediately above, fig. 53. In a transverse section through the filament of Saxonia, the



Heider (10) has figured the lateral parts of the filaments as composed of just such large granular cells, as I have described. The Störwig also speaks of these tracts.

The filaments on the secondary mesenteries are somewhat smaller than those on the primary mesenteries. The mesenterial lobes are less pronounced, not reaching a development greater than is shown in fig. 54. It has been mentioned that in the upper part of their course the secondary filaments become very small. Though the diminution in size is so great in this region, that it was impossible for me to make out the histological structure, I was able to trace the filaments as a densely staining and compact mass of tissue into the epithelium of the peristome. The filaments in the young coral in which figs. 41 & 42 were made, were like the adults, except that the mesenterial lobes had not reached a development beyond that in fig. 54.

I did not study the living filaments, but from the histology it is evident that the function of the ventro-lateral tracts is that of ciliated bands, while





The ~~first~~ digestive functions, and rectal cells, are distributed over the three portions of the main body of the filament. The mesobial lobes I regard merely as a device to support the filament.

Before comparing the mesobial filaments of Thamna with the Actinian filaments as described by the Harkings, I will give a brief account of the filaments of Cerianthus, this being the only Actinia I have been able to study by way of comparison. In the Nassau Harbor the larval or pre-swimming Cerianthus was common. All the individuals I obtained were at about the same stage of development. They <sup>were</sup> had oval light brown bodies about  $\frac{1}{3}$  in. long, and had eight or nine very short, stubby bristles. On sectioning the larvae I found they confirmed the theory advanced by the Harkings (l.c.) as to the mode of origin of the mesenteries. Fig. 49 is a section through the upper part of the oesophagus. The number of complete mesenteries is fifteen. At one end of the oesophagus is the ventral or directive pair of mesenteries, 2 in. At the other or dorsal end are two incomplete mesenteries



1 + 2, of which the former is the younger. The mesenteric 3 becomes incomplete not far above the oesophageal lip, and 4 follows its example just above the lip. From these four mesenteries it may be gathered that each new mesenteric appears along the dorsal meridian between the two last formed, and in such a way that the successive mesenteries come to lie on opposite sides of the dorso-ventral plane. The directive pair D.M. corresponds, it would appear, to the directive pair which the starlings have figured (Tot, fig. 8). These authors state however that this pair is the longest of all, extending to the anal pore. In the young specimens I have studied, this pair disappears some distance above the pore and is exceeded in length by two or three mesenteries on each side of the dorso-ventral plane. Van Heider (11) made the discovery, which the starlings confirmed, - that in the adult there is a much shorter pair enclosed between the two directive mesenteries. This short pair only extends the length of the rectum. It must appear in stages later than fig. 40, as



that besides the formation of mesenteries which takes place dorsally, at least one pair is formed ventrally.

Filaments were found only in the complete mesenteries. Fig. 47 is from a section just below the oesophagus. The mesentery is composed of very large cells with immense vacuoles. At the edge of the mesentery, just beneath the filament, the tissue is becoming more compact. This process has gone much farther in fig. 48 (from the same mesentery at a lower level). The whole mesentery, as may be seen by comparing my figures with Hertwig's Taf. VIII, gradually suffers this change as the animal becomes adult. In fig. 47 the filament has a central body provided with gland and needle cells, and two lateral ciliated tracts m, into which the jelly begins to extend. The central body passes directly into the epithelium of the oesophagus, the lateral tracts becoming indistinguishable from the body of the filament just before the transition. This figure is but slightly different from the section of the adult filament given by the Hertwigs. At a



lower level, fig. 48, the ciliated tracts are no longer found. On many mesenteries the filament has almost no connection with the endoderm, as in the figure. In such figures as 48, it need hardly be said that violent contraction has had much to do with producing such complete separation of filament and mesentery; but this only shows how loose the connection is in early life. On other mesenteries the filament is continuous at its sides with the cells of the mesentery. None of the filaments in these young specimens of Cerianthus ran the whole length of the mesentery. Most stopped at about the equator of the body.

In six Aclines studied by the drawings the mesenterial filament in the upper part of its course is in section tri-lobed: There is a median secretory tract, and two lateral ciliated tracts. The mesoderm extends into each lobe. On all the mesenteries the ciliated tracts are lost in the lower portion of the filament. On the incomplete mesenteries the median tract disappears towards the upper limit of the mesentery, the lateral





ciliated bands remaining. On the complete mesenteries the median tract merely gets smaller towards the ventral end, but does not disappear.

The description I have given of the filaments of Cerianthus is, barring slight differences due to age, quite like the account the Herwig's give for this Actinia. From this description it is seen that the filament of Cerianthus corresponds in the main to a typical bryozoan filament, such as is on a complete mesentery. But the lateral lobes, in fig. 47, are very small even in the adults, when compared with the lateral wings of the Sagartia filament (H. Taf. V, fig. 10)

The filament of Manicaria is a much simpler structure. It is not bifid, though the mesenterial lobes, m. l. fig. 52, give such an appearance to the edge of the mesentery. But in referring to Herwig's figure of Sagartia (Taf. V, f. 10) it is evident that the mesenterial lobes of Manicaria do not represent the ciliated bands of Sagartia: they are structurally distinct, and do not contain intercalations.



the mesoderm. On the other hand the ventro-lateral tracts of Manicaria do correspond histologically with the ciliated bands in the Hertwig filament, and the glandular lobe of the latter is in general similar to the body of the Manicaria filament. As I take it, all three tracts of the Hertwig filament, taken together, are homologous with the simple filament of Manicaria. They must all therefore be ectodermal: in the young Cerianthus, fig. 47, the lateral lobes evidently belong to the median lobe and are not modified parts of the mesentery; but the median lobe at a lower level, fig. 48, shows its independence of the mesentery; the conclusion is that the whole filament is ectodermal. Though the filament of the adult coral is a much simpler form than the bifid filament, it would be difficult to derive the latter from the former owing to the presence of mesenteric lobes in the coral. It is easy however to derive the bifid filament from the larval filament, fig. 35. In this form the ciliated tracts, v.l., and the median secretory tract, are already differ-



entiated; to produce the bipid filament, it is only necessary for these tracts to become separated by the division of the mesoderm into three lobes. By this division, while the median stripe gains but little, the ventro-lateral tracts are put in a position where it is possible for them to reach a high development.

The number of Actinopora in which the mesodermal filaments have been carefully studied is very limited, but from the data at hand it seems probable that the ancestral filament, like the filament of the larval Manicina, was a single undivided body, in which however the originally uniform ectoderm had become split up into three physiologically distinct tracts: a median tract in which were concentrated the nettle and glandular elements, and which embraced most of the filament; and two lateral ciliated tracts which were but slightly developed. The belief that the division of labor in the <sup>Zoantharian</sup> ~~Actinopora~~ filaments dates very far back, is supported by the existence of a similar division of labor in the Alcyonaria. But in



These polyps, as Wilson (8) has shown, the functions are not distributed over different parts of the same filament; but amongst the several filaments. The dorsal hair are ciliated bands, having no gland or nettle cells, while the remaining six filaments contain gland and nettle cells, but have no ciliated tracts.

#### VIII. Skeleton.

VIII.

Until the time of von Krich's researches the skeleton of the Madrepuraria was regarded as calcified mesoderm. The theca or coral wall according to this view represented the supporting lamella of the lateral body wall of an Actinia; and where, as in most corals, the theca was largely uncovered by animal substance, the explanation was that the ectoderm had atrophied. In 1879 von Krich (12) showed that the theca is independent of the lateral body wall, and projects into the general cavity of the polyp in such a way as to divide the cavity and mesenteries into central and peripheral parts. This





conclusion though not universally accepted is I  
 think now incontestable. Van Heider in 1882 (14) pub-  
 lished the important observation that the skeleton  
 is not only covered by supporting lamella and  
 endoderm, but that between the calcareous matter  
 and the supporting lamella is another layer of  
 cells to which was given the name of calicoblasts.  
 Von Koch in 1883 (13) made the whole matter clear  
 by showing that in the young Asioides the skele-  
 ton is secreted by the ectoderm, and is at first  
 entirely outside the body. The ectoderm of the bu-  
 ral surface of the attached larva secretes a calca-  
 reous basal plate. Radial folds of the basal ec-  
 toderm then grow up between the mesenteries into the  
 cavity of the polyp, lifting up as they grow the sup-  
 porting lamella and endoderm. The cavity of the fold  
 is filled with calcareous matter, which is the sep-  
 tum. The remaining ectoderm becomes the calico-  
 blast layer of von Heider. The origin of the basal  
 plate and septa is thus clear enough, but von Koch's



account of the development of the theca is not satis-  
 factory. As far as his observations went they appear  
 to have confirmed his belief, gathered from a  
 study of the adult corals, that the theca is  
 formed secundarily from the septa in the follow-  
 ing manner. The septa originally simple radial  
 lamellae either become bifurcate at their peripheral  
 ends, or acquire lateral outgrowths at these ends  
 so that in section they are dagger shaped. The  
 lateral processes (hills of the dagger) of adjacent  
 septa grow towards each other, pierce the mesentery,  
 and fusing form the theca. Van Korch's account  
 of the relation of the skeleton to the soft parts in  
 the adult, has recently been confirmed on a num-  
 ber of genera by Fowler (15) and Bourne (16), though  
 from these papers it is evident that there is a great  
 variety of detail in this matter among the Mad-  
 agascaria. My own very incomplete observations on  
 the skeleton of Manicaria are for the most part  
 a confirmation of van Korch's statements.



In the newly attached larva, fig. 37, the ectoderm of the basal surface is made up exclusively of supporting cells. The granular cells present at the dorsal end of the swimming larva have all disappeared. Some time after attachment a small patch of calcareous matter is made on the basal surface, and sections through such larvae, after the lime has been removed by acid, give figures like fig. 38, though in many individuals the ectoderm was torn in tearing the larvae from the bottom of the dish. In fig. 38 the cells of the basal ectoderm radiate towards a common center. There seems to be an effort on the part of the more peripheral cells to share in the secretion of the central patch of homogeneous substance shown in the figure. This homogeneous substance is the animal basis of the resorpt-basal plate. It exhibits no structure, but stains deeply with hematoxylin, and in its general appearance impresses one as a very much thickened cuticle. I was not able to trace the development of the



skeleton any farther.

The fully formed skeleton may very conveniently be studied in young polyps which have not begun to multiply asexually. Ground sections of the skeleton are of some use, but with a little care the polyps may be decalcified so that the skeletal layer of tissue retains with great exactness the shape of the skeleton. Figs. 45, <sup>156,</sup> & 50, are from a young *Manicيرا* about  $\frac{1}{3}$  in. diam. Fig. 46 is part of a transverse section through the line a in fig 50. <sup>(oc. ec. in the ectoderm of the peristome, ec. that of the lateral body wall).</sup> ~~The polyps, which are not ready.~~ Here the section is complete, it would show twelve primary, twelve secondary, and twenty four tertiary bands of mesenteries. At this level the secondary mesenteries are complete. In going down through a series of sections the tertiaries ~~run~~ run out before the tip of the oesophagus is reached: in fig 50 the line 3, on the left side, marks the free edge of a tertiary mesentery, which unlike the secondaries, is ~~not~~ provided with a filament. The Th, Th, divides





the mesenteries and gastric cavity into peripheral and central portions. The septa  $\delta$  are all entocellular, i.e. lie between the two mesenteries of one pair, and not between two adjacent pairs. The size of the septa varies with the range of the mesenteries between which they lie. On the outer side of the theca are the longitudinal ridges  $\epsilon$ , or costae, which appear to be merely the peripheral prolongations of the septa. The edges of the septa and costae are finely and regularly beaded. This is shown in the radial section fig. 56, which is taken through one of the coral septa. In figs. 57 & 58 the relations of the columella, col., to the theca and septa are shown. In the main figure, through a mesentery on each side and consequently between two septa, a deep depression separates the columella from the theca. The primary mesenteries extend to the floor of the depression, the secondary end some distance above it. The columella is circular in section, and the depression encircles it as a trench. But



The tract is not continuous, being completely divided in the radius of each primary septum, as is gathered from fig. 38 which is taken through such a septum. In this figure the septum and columella are directly continuous with each other. The columella in reality is not solid, as it is drawn in the figure, but is spongy, being full of portions of the body cavity which it has cut off during its growth. Whether an originally simple and solid columella is formed as a central elevation of the basal plate, is an open question. But the subsequent growth of the columella takes place by the constant incorporation in it of the lower portions of the inner edges of the primary septa. The teeth on the edge of the septa and the small protuberances found on their sides, sufficiently explain the spongy nature of the columella.

The skeleton inside the polyps is everywhere covered by the three layers of the body wall, of which the sclerogenous ectoderm or calicoblast-layer is next the skeleton. In fig. 46 and the radial



sections these layers are not represented, but they are shown in fig. 57, a more highly magnified portion of one of the peripheral enterocoele (between two mesenteries of one pair) chambers of fig. 46. The superficial ectoderm is marked ee, the peripheral parts of the mesenteries mes. The calicoblast layer covering the costae, or more exactly the costal wall, as it is elsewhere a layer of flattened cells the skeletal ectoderm is likewise very flat, and markedly different from the ectoderm of the body wall and mesenteries. In radial sections the calicoblast layer is found to be continuous with the superficial ectoderm round the edge of the extra-skeletal part of the polyp or radial plate, R.P. in fig. 50.

That portion of the polyp which lies outside of the theca, R.P., has been called by von Heider the radial plate. It has been claimed (Fowler, 15-1) that this part of the polyp ought not to be regarded as normally on the outer side of the skeleton, but that it is part of the oral surface which owing to dis-



which has been pulled down over the skeleton. This  
 belief is at once found to be reasonable on examining  
 a small number of young Maniceras of about the  
 size of fig. 50. In the polyp, for instance, from which this  
 section was made, the sand plate covered more  
 than one half of the lateral surface of the skeleton,  
 and this was true both in the expanded and contracted  
 condition of the animal. Further in every dozen  
 such young Maniceras, one or two asymmetrical ones  
 will be found, in which while the sand plate is  
 confined to the upper half of the lateral surface  
 on one side of the polyp, on the other side it covers  
 the whole way down to the surface of attachment.  
 What gives the matter beyond dispute, in this genus at-  
 least, is that in the <sup>very</sup> young Manicera, figs. 41 & 42, the  
 whole skeleton is practically inside the polyp. I also  
 found two or three older specimens (single polyps) in which  
 the entire lateral surface of the skeleton was cover-  
 ed by the sand plate. One of these, which I sec-  
 ured, was oval in transverse section, long axis





about  $\frac{2}{5}$  in., short axis  $\frac{1}{4}$  in. The skeleton had a fleshy surface & attachment, and was 3 in. in height. The sand plate in this individual was unbroken down to the inner & next, to which the coral was fastened; ~~and~~ <sup>there</sup> it <sup>continued</sup> turned in, to form the calicoblast layer.

It appears then that up to a certain age, which I think varies much in individuals, the lateral surface of the skeleton is entirely covered by the polyp. The transformation of the originally large extra-thecal part of the polyp into the relatively small sand plate may possibly take place <sup>in many cases</sup> gradually, by the constant dying off of this part of the polyp at its free edge and subsequent disappearance of the dead tissue. But in some instances this is not the case. I found a number of small single polyps in which I first thought the sand plate covered the entire lateral wall of the skeleton, but on looking again I saw that a very definite line extended all round the lateral surface at about the level of the edge of the sand plate in fig. 50. Above this line the soft-



parts looked perfectly healthy, but below it died and  
 decayed. On sectioning I found that above the line the  
 sand plate was normal, but that the tissue below it  
 was a membrane with scarcely a trace of cellular  
 structure and made up for the most part of plant  
 filaments. In some symmetrical specimens the portion  
 of the section left uncovered by the sand plate,  
 was covered by a precisely similar membrane  
 which was raised off from the sand plate by a deep  
 furrow. In all such specimens the <sup>extremity of the</sup> sand plate was  
 continuous at <sup>the</sup> ~~its~~ <sup>of the latter</sup> edge with the calycoblast layer.  
 These peculiar membranes gave every appearance of having  
 been originally continuations of the sand plate; and  
 I conclude that in the individuals possessing them,  
 the extra-thecal part of the polyp had remained  
 intact up to a certain time, but that then the whole  
 lower portion of this part of the animal was cut off  
 from the general gastric cavity. Deprived of its nutri-  
 ment this part became membranous and  
 was infested by plant filaments. As the coral



increase in size the membranes are shed, leaving a large part of the Theca bare. After the rind plate has become restricted to the upper part of the skeleton, there is no more shedding of large pieces of tissue. But as the skeleton is constantly growing in height, we have to suppose that the rind plate is constantly ~~new~~ at its free edge, unless indeed we assume that the connection between the calcareous layer and the skeleton is so slight that the rind plate is merely carried up with the growing skeleton.

In the young *Meridia*, figs. 41 & 42, which was  $\frac{1}{8}$  in. diam., the skeleton is very immature, though the various parts of the adult skeleton can all be recognized. In this specimen there was a thin, flat basal plate, uncovered at its periphery by the body wall. The skeleton above the plate was internal except at the points a and a', where the lower edge of the lateral body wall was notched, so that at these points the skeleton was bare for



a short distance above the basal plate. Fig. 41 is through the esophagus; fig. 42 is below, and crosses the apex of the columella. Though some of the septa are still independent or as low a level as fig. 42, at a still lower level they all unite to form a theca, which on the right side of the directive mesenteries is very slightly developed, but on the left side is prominent. Two or three of the septa in the region where the theca is so slightly developed, exhibit the bifurcation of their peripheral ends which Lacaze Duthiers and von Koda Ick described. In fig. 42 indications of six primary septa are more or less evident, and in lower sections where the septa fuse with the columella, ~~these~~ <sup>they</sup> ~~six~~ are easily distinguished. There are also six primary septa to be made out in fig. 42, <sup>which are entocœlic</sup>. Then twelve septa, extend as high and higher than fig. 42. Further in fig. 42 it is evident that twelve tertiary septa have started to develop, though only a few of them extend an appreciable distance above the theca. As only twelve pairs of mesenteries have been formed,





The tertiary septa are temporarily excessive. Transverse and longitudinal sections through such a polyp as this, show very clearly that the growth of the theca is continuous and from below upwards. Nowhere are the septa found which actually pierce a mesenteric from the theca, but everywhere the growing theca pushes the tissues of the mesenteries upwards. Where the theca is formed in such a manner as this, it is not of the question to believe, after von Knoch, that the radial cracks found in ground sections of the theca are due to the existence in these radii of the atrophied remains of the lower portions of the mesenteries.

The corals in figs. 41 + 42 are very feebly and irregularly developed. Each septum has however three or four teeth along its outer edge and also a few on its inner edge. All the teeth on the outer edge of the septa open directly to the exterior over the side wall of the coral. In fig. 41 the septum included between the two pairs of directed mesenteries, is cut just below the point at which it thus passes.



Fig. 40 gives a more highly magnified view of the same septum cut at the level of its opening. In fig. 42 a tooth has opened at  $m$ , and another at  $n$  is sedimented just beyond its opening. The openings are of good size, and though then the external ectoderm is continuous with the calicoblast layer. This peculiarity of the teeth is no longer found in *Manicera* after sexual multiplication has begun, and only a few teeth open to the exterior in single polyps with the full complement of septa. In one such polyp however all the teeth opened in this way. From this it would seem that the connection of the calicoblast layer with the external ectoderm at these points, is a characteristic of youth which is gradually lost. It is possible that this peculiarity may have been acquired, in order to serve the little polyps and its single skeleton to be together.

#### IX. Origin of the Anthozoa

As is well known the reigning view as to the origin of the Anthozoa is that advanced by Claus and



and Haeckel, according to which the Anthozoa are descended from hydrozooids with gastric ridges. This hypothesis which considers the distinguishing feature of the Anthozoa (and Scyphomedusae) to be the possession of tentacles or endodermal ridges, has recently been attacked by Prof. Götze in a very interesting paper<sup>(19)</sup> on the development of the Scyphomedusae (Urellia!). The author conclusively proves the Anthozoan nature of the Scyphostoma larva, showing it to possess four complete mesenteries and an ectodermal oesophagus. Unfortunately no observations were made on the origin of the mesenterial filaments, which in all probability are ectodermal lobes. Regarding then the Scyphomedusae as an offshoot from the older Anthozoan stem, Götze argues that the manner in which the mesenteries and intramesenterial chambers are formed in the larva of the former, is directly opposed to the old view of the hydroid origin of the Anthozoa. The mesenteries and chambers are formed in the following way. The <sup>planula</sup> larva is markedly bilateral, and the



permanent layers are formed before the invagination of the oesophagus takes place. The latter is invaginated in such a shape that in the shorter transverse axis of the larva the endoderm is pushed down, while in the other transverse axis two endodermal poles are formed. The wood cut fig. 1 is a transverse section of this stage through the oesophagus, and fig 2 is a longitudinal section through the shorter transverse axis. In a subsequent stage two endodermal poles grow up from the general gastric cavity in the shorter ~~trans~~ axis, and the oesophagus is then surrounded by four poles. These poles are the intramural chambers and their partition walls form the mesenteries. Götze concludes that in this development there is no stage which corresponds to the hypothetical hydroid ancestor. The <sup>young</sup> Scyphostoma itself which has hitherto been regarded as a hydrozoan with tentacles, is in reality an Anthozoon with four mesenteries, and the development previous to the Scyphostoma does not pass through a hydroid stage, but on the contrary jumps directly





from a hollow planula to the larva invested with two (later four) endodermal sacs. This larva is called the Scyphula, and from Kowalevsky's account of the development of Cerianthus, Götze believes it to be common to both the Scyphomedusae and Anthozoa, and consequently an ancestral form. In Cerianthus, according to the abstract given by Hoffman & Schvalbe of Kowalevsky's paper, the oesophageal invagination does not down the endoderm along two opposite meridians, but the abstract seems to imply that these are the meridians of tubular mesenteries. If this is so, Cerianthus agrees with Manicaria, and not with Aurelia.

The ancestral Scyphula form was derived, according to Götze, directly from the hollow planula; the invagination of the oesophagus necessitating the simultaneous formation of endodermal sacs. The intra-oesophageal mesenteric ridges, from this point of view, are not of any phylogenetic importance, and have nothing to do with the endoderm ridges of Tubularian or Siphonophore polyps; they have come into existence merely as



the after results of the formation of endoderm sacs. This theory contains in itself an obvious difficulty: the sudden and direct transformation of such a simple form as the planula into such a complex form as the Scyphula. What could have caused this complex <sup>group</sup> series of changes, Gille does not suggest. But aside from this objection, it seems clear that the development of Aurelia is a highly modified form of the development of Manicella, and the manner in which this peculiarly asymmetrical modification was brought about, is suggested by the variation shown in figs. 30-32.

If fig. 30 is compared with the woodcut fig. 1, it is seen that as far as the left halves of the sections are concerned, they are identical in all essential respects. In each the oesophagus is apposed to the superficial ectoderm not only along the meridians of two adjacent mesenteries ( $a + b$ , 1 + 3) but over the intervening tract also. In a later stage an endoderm lobe grows up between  $a + b$  in fig. 30, and between 1 + 3 in the woodcut, and in each this lobe be-



covers an intersegmental chamber. If now in the larva figs 30-32, the right side had followed the example of the left, that is if the second and third mesenteries had been formed in the same manner as the first and third (a & c), there would have resulted an exact counterpart of the condition in the Aurelia larva.

The four mesenteries of Scyphostoma would thus seem to correspond to the first and second pairs of mesenteries of Manicaria. We may suppose that in the primitive Scyphostoma the mesenteries were usually formed in the gradual way, which is normal in Manicaria, but that the Scyphostoma had inherited from the parent stock (probably Anthozoa with a large number of mesenteries) a tendency towards the variation illustrated in figs. 30-32, and that this variation gained ground and finally became the normal process. There is of course an alternative to this hypothesis, namely to regard the variation found in Manicaria as a case of partial reversion to the ancestral condition as presented



by Benda. But the derivation of the Anthozoa from such an ancestor as the young Scyphostoma (or Scyphula with four everted lobes) is beset with the greatest difficulties, for instance the formation of the first before the second mesenteric, and the very general occurrence of a primary intacle in Actinea larvae and in the Scyphostoma itself. Moreover the Scyphula larva has not been found in any Anthozoa, unless indeed the case of Criarthus be really as Prof. Gille seems to have considered it.

Having shown that it is possible to derive the so-called Scyphula larva from the larva of Monicaria, and that it is consequently in all probability an instance of secondarily acquired symmetry, I consider Gille's objection, based on the existence of this larva, to the hydros. polyps ancestry of the Anthozoa, as no longer valid. The question whether or not the Anthozoa are descended from hydros. polyps must be argued out on the ground of some more primitive Anthozoan development, such as that of Monicaria. And here it is





as was seen that, contrary to Götts idea, the invagination  
of the oesophagus does not necessitate the formation of  
extra-dorsal pairs. In figs. 5+7 the oesophagus is already  
formed, but is still surrounded on all sides by ex-  
oderm. The apposition of the oesophagus to the superficial  
ectoderm along the lines of the first and second segmen-  
tary lines takes place later; and though, since this pro-  
cess occurs in the *Scyphomedusae* as well as in the  
*Lanthornia*, it must date very far back, I am in-  
clined to believe that it was secondarily acquired  
and was not a peculiarity of the primitive Antho-  
zoa. This belief is supported by the entire absence of  
the process in the *Aequorea* (Wilson, 3). The explana-  
tion of the process is possibly connected with the  
early development of the first pair of filaments.



X. Systematic Description of Mariccia.

X.

Milne-Edwards names Mariccia the sixty fourth genus in the family Astracidae. Like Meandrina this coral grows by incomplete fusion, the calices remaining connected so as to form meandering valleys, in which the limits of a calice are not distinguishable. The shape of the colony ordinarily met with is subtriangular (see figures on Pl. 1), there being a well marked pedicel. With increasing age the pedicel becomes less and less evident, until the corallum finally assumes the shape of a convex mass with a flat basal surface. The basal surface has two diameters, the longer about three inches, the shorter two inches, and the vertical height of the corallum is about equal to the shorter diameter. The distinguishing features of the genus besides its growth from a pedicel, are as follows. The columella is spongy and very well developed. The septa are thin, closely set, and have very strongly marked granulations on their sides. The edges of the septa turn within and over the exterior of the calices, corals!



are finely and regularly toothed. "The genus was named in honor of E. H. Emery, for certain of *Sarcophaga Mendocini* are characterized by growing from <sup>a radial or</sup> a central point of attachment" (Dana). In the species *M. aridula* the septa can be divided into three cycles, and each septum has in the neighborhood of the columella a large and rounded lobe.

The animal is of a brownish color, and when expanded extends high above the pscellum. In this condition the tentacles are moderately long, and are closely set round the periphery of the oral surface. In the pedunculate forms, both in the expanded and contracted condition of the animal, the upper part of the lateral surface of the pscellum is covered by the fold. The pedicel which includes the pscellum below this region is usually disfigured by small annulated tubes and other incrustations.

The young, after the swimming life is over, affix themselves to some solid substratum such as a piece of wax or a shell. To this they remain



attached, until they have reached a diameter of about half an inch. In this condition they are single polyps circular or oval in transverse section, and with a flat or irregular surface of attachment. The multiplication by fission then begins, and with it the formation of the pedicel. When the latter has become apparent, the coral is broken off from the rock to which it is attached, and fragments sink into the sand.

Baltimore, Mar. 21, 1888.





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## Description of the Figures.

All the sections were drawn with the camera. In the larvae the supporting membrane is represented as a heavy black line, the gills (when present) as light brown. <sup>in the figures & Coriaria</sup> In the adults, the supporting substance is left uncolored, except in figs. 47 & 48. Lens boxes were used, and the figures are reduced to one half of the size of the original drawings.

The following letters have been used uniformly in the figures:

c. b.	Calycoblast Layer
en.	Endoderm
ec.	Ectoderm
D. M.	Director Membranes
S	Septum
C	Coxia
Th	Theca
Col.	Columnella
T	Tentacle
Pr.	Peristome





Mo.	Mouth
Oe.	Oesophagus
R.P.	Rand. plate or Extra-thecal part of the polyp.
m. l.	Mesenterial Lobes
v. l.	Ventr. lateral Ciliated Tracts
Mes.	Mesenteries.

### Plate 1.

- Fig. 1. Section through a blastophore. C, 4.
- " 2. Delaminating blastophore. C, 4.
- " 3. Part of another blastophore such as f. 2. D, 4.
- " 4. Median long. sec. through a solid planula with commencing oesophagus. C, 4.
- " 5. Median long. sec. through a larva in which the permanent layers are forming. C, 4.
- " 6. Long. Sec. of slightly older stage. Position of oesophagus is extreme. C, 4.
- " 7. Trans. Sec., through oesophagus, of larva at about the stage of fig. 5. The formation of the permanent layers is not as far advanced as in



- \* The latter figure. 2, 4.
- " 8. Long. Sec. Through larva in which the oesophagus has opened centrally. D, 4.
- " 9. Trans. sec. Through a larva in which the oesophagus is still more eccentric than in fig. 8. The section is through line a in f. 8. D, 4.
- " 10. Trans. sec. of same larva at lower level - through line b in f. 8. D, 4.

### PLATE II.

- Fig. 11. Transverse section, through lower part of oesophagus (primary ectoderm lobe) of a larva, in which the oesophagus along its whole length was applied to the superficial ectoderm. D, 4.
- " 12. Long. Sec. of larva at about the same stage as f. 11 - in the plane of the first two main lines. D, 4.
- " 13. A section to one side of f. 12 - through lateral intersegmental chambers. D, 4.
- " 14, 15, 16, & 17. A series of transverse sections,



numbered from above downwards, from a larva in which the first pair of filaments, and the first mesenteric ridge, have been formed. Along the line of mesenteric 2, the oesophagus is still applied to the superficial ectoderm. Fig. 14 is through the oesophagus. D, 4.

Figs. 18 + 18 a. Trans. <sup>sections</sup> ~~seen~~, through oesophagus, of a larva with two complete mesenteries and a pair of filaments. Fig. 18 a is the upper of the two. D, 4.

" 19. Surface view of Balsam preparation. The larva has two long, and one (possibly ~~two~~ <sup>one</sup>) short filaments. C, 2.

### Plate III.

Figs. 20, 21, 22, + 23. A series of longitudinal sections from a stage somewhat younger than f. 18. Fig. 20 is through the first pair of mesenteries and filaments, fig. 23 is through the line a-b in f. 18, and the other two sections fall between. C, 4.

" 24. Long. sec. through a larva such as fig. 19 - on



the right through one of second pair of filaments, on  
the left through an intersegmental chamber. D, 4.

Fig. 25. The larva has two long and two very short  
filaments - a, b, + c are three half-sections. b is  
through one of the second pair of mesenteries with  
its filament; a + b are on opposite sides of this  
mesentery. D, 4.

" 26. Trans. sec. through one of primary pair of fila-  
ments and mesenteries of a stage like f. 19. F, 4.

" 27, 28, 29. Series of transverse sections from a larva  
like f. 19. Fig. 27 is through the oesophagus, 28 is  
just above the lip, and 29 is below the oesopha-  
gus. The third pair of mesenteries have appear-  
ed. R.E. is the reflected ectoderm. D, 4.

#### Plate IV.

Figs. 30, 31, 32, 33. Series of transverse sections, num-  
bered from above downwards, through a larva  
with two pretty long (half the length of larva!) and  
one very short filament. The first and third





filaments are joined from a common tube, and the third mesenteric (b) is joined at the same time and in the same way as the first (a). D, 4.

Fig 34. Trans. sec., below the oesophagus, of attached larva with 8 mesenteries. B, 4.

" 35. Trans. sec. Through upper part of one of primary filaments of attached larva. The large clear cells are niddle cells. T, 4.

" 36. Trans. sec. of attached larva with 8 mesenteries - Through the oesophagus. The second pair of mesenteries is not quite complete, so that at this level the reflected ectoderm is found all round the oesophagus. B, 4.

" 37. Median long. sec. Through attached larva - on the right - through one of second pair of mesenteries, on the left - through an intermesenterial chamber. C, 2.

" 38. Median long. sec. Through attached larva in which the basal plate has appeared - on the left - through one of third pair of mesenteries <sup>with</sup> and



its filaments; on the right through an intersegmental chamber. The line m-m indicates the outline of the animal when expanded. C, 2.

Fig. 39. Trans. sec., through oesophagus, of attached larva with 2 mesenteries. B, 4.

" 40. Section through one of the caeca of fig. 41, which at this level opens to the exterior. c. b. is the calycoblast layer.

# Plate V.

Fig. 41. Trans. sec., through oesophagus, of young Monocira  $\frac{1}{8}$  in. diam. D.M., digestive mesenteries.  $\times 60$ .

" 42. Section of same individual, below the oesophagus. Skeleton is bare as a and a. Tip of columella lies in gastric cavity.  $\times 60$ .

" 43, 44, 45. Series of transverse sections, numbered from below upwards, through the oral cone of a larva like f. 38. Fig. 43 is taken through the line x-y in f. 38. In this individual only the first two pairs of mesenteries extend into the



uppermost part of the column. The overlapping of  
the reflected ectoderm and endoderm is well  
shown. D, 4.

Fig. 46. Part of a transverse section of an adu-  
single polyp, through the line a in f. 50. The  
ectoderm of the peristome is marked ec. ec., that  
of the lateral body wall ec. Th is the theca,  
S a septum, C a costa. X 30

" 47. Trans. sec. of filament and mesenteries of a  
larval *Cnarianthus*. Level of section is just  
below the oostegium. m is the commencing  
ciliated band (Humerus!). F, 2.

" 48. Section of same filament, lower down. The  
violent contraction has caused the halves of the  
mesenteries to spring apart, leaving the coga-  
lated supporting lamella more or less free.  
F, 2.

" 49. Trans. sec., through oostegium, of a larval  
*Cnarianthus*. D.M., the 'larval' digestive mesen-  
teries. The numbers 1, 2, 3, 4, mark the four



youngest numerus, in the order of their age, being  
the youngest. X 60.

### Plate 11.

Fig. 50. Median long. sec. through an adult single  
polyp., on the right through a primary, on the  
left through a secondary mesenteric. The line 3  
waves the free edge of a tertiary mesenteric. The  
surface of attachment was irregular, but the  
coelom extended only a very short distance  
below the limit of the coelom in the figure. X 30.

" 51. One of the extra-thecal extracoelomic cham-  
bers of f. 49, more highly magnified. M.C. is  
the peripheral portion of a mesenteric.

" 52, 53, 54. Transverse sections of an adult  
primary filament. Fig. 52 is through the upper,  
53 through the middle, and 54 through the lower  
portion. M.C. is the mesenteric coelom, V.C. the  
ventro-lateral ciliated tract. The large clear  
cells in f. 53 are nettle cells. D, 4.





Fig. 55. A more highly magnified figure of the lower portion of the oostegium as shown in the left half of fig. 54. l. ec. is the living epithelium of the oostegium.

" 56. One half of a median long. sec. of an uncalcified single polyp. The section is through one of the very narrow septa.  $\times 30$ .







H.V.W. del.

Plan ..





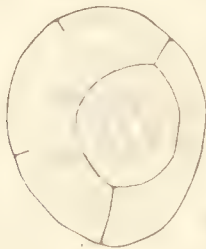






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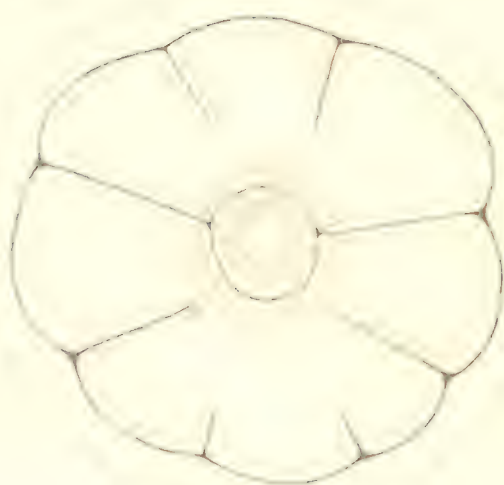
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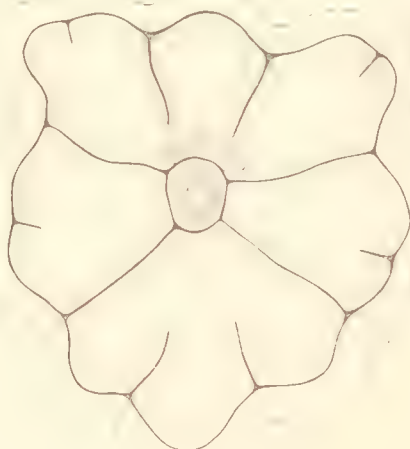
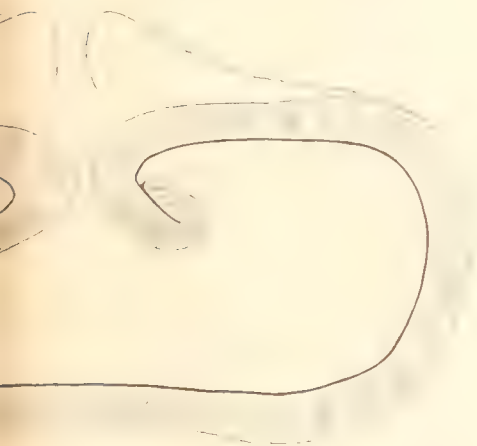




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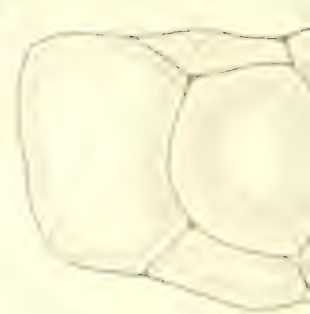


10-10-10  
10-10-10









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